Niche partitioning in sympatric *Sarracenia* species at Splinter Hill Bog Preserve, Baldwin County, Alabama

Jacquelyn S. Howell • Department of Biology • University of South Alabama • Mobile • Alabama • USA
Ashley B. Morris • Department of Biology • Middle Tennessee State University • Murfreesboro • Tennessee • USA • amorris.mtsu@gmail.com

Keywords: Ecology, *Sarracenia*, Splinter Hill Bog Preserve, Alabama.

Abstract: With anthropogenic influences limiting and fractioning wetlands, it is imperative to understand niche partitioning in keystone species. *Sarracenia* (Sarraceniaceae), a genus of carnivorous plants, are ecologically important species found in wetlands along the eastern coast of the United States. Species diversity of this genus is highest in the southeast, particularly along the Gulf Coast where they are found primarily in longleaf pine savannas. This study aims to identify underlying causes driving niche partitioning, specifically exploring water table elevation and soil type as potential sources. Splinter Hill Bog Preserve, located in northeastern Baldwin County, Alabama, served as the study site for this work. Findings indicated small, but significant correlations between soil type and species distribution, as well as between soil type and water table elevation.

Introduction

Niche partitioning has been informally documented in sympatric species of North American pitcher plants, *Sarracenia* (Sarraceniaceae), over the last several decades. Niche partitioning is the process by which natural selection acts upon organisms and allows closely related species to inhabit different environments or microenvironments. Although many reports allude to obvious habitat differences (shade, soil moisture, *etc.*) to explain distribution of species in sympatric *Sarracenia* populations (McDaniel 1966; Gibson 1983; Schnell 2002; Mellichamp 2009), few empirical studies have evaluated the underlying factors driving niche partitioning among species.

Eleven species (*S. leucophylla*, *S. purpurea*, *S. psittacina*, *S. rubra*, *S. flava*, *S. alata, S. oreophila*, *S. minor*, *S. alabamensis*, *S. jonesii*, and *S. rosea*) and several subspecies and varieties of *Sarracenia* are currently recognized (Ellison *et al.* 2012). One species, *S. purpurea*, radiates up the east coast, across the northern U.S. and boreal Canada west to British Columbia (Sheridan 2010). In the southeastern U.S. (Florida, Georgia, Alabama, Mississippi, and Louisiana), where *Sarracenia* species are found in sympatry, hybridization is common (Furches *et al.* 2013) and niche partitioning is prevalent (pers. obs., JSH).

Closely related sympatric species may still have slight differences in microenvironment requirements (e.g. salinity, elevation, pH, *etc.*; Welch & Rieseberg 2002). These differences are not only important for a species' ability to expand its range and to compete for resources, but they can also be important from an evolutionary perspective. If hybrids are able to utilize adaptations from parent species and potentially occupy habitats that are not optimal to either parent species, there is increased opportunity for spatial isolation that could promote speciation over time (Arnold *et al.* 1991; Edwards-Burke *et al.* 1997; Milne *et al.* 1999).

Soil characteristics have been shown to influence wetland plant species composition in pitcher plants bogs in the Little River Canyon National Preserve in Alabama (Carter *et al.* 2006). The unique geology and hydrology of bogs, in particular southern pitcher plant bogs, may be the underlying cause of observed niche partitioning in sympatric *Sarracenia* species. Southern pitcher plant bogs are typically made up of sandy soils, with the water table just below or at ground surface level. In some cases, shallow clay layers (i.e., aquicludes) that allow water to accumulate may cause local areas of saturation in places with deeper water tables (Plummer *et al.* 2001). These aquicludes, as well as other hydrological and geological influences (e.g., water-table elevation, soil types, *etc.*), may be sources of variation in plant species distribution in a seemingly homogenous habitat.

The most extensive study of distribution patterns in *Sarracenia* (and other carnivorous plants) was by Gibson (1983), who proposed there would be negative associations between species of similar heights, as more pitchers at the same height increases competition for insect prey. Although *Sarracenia* species use passive traps to capture prey and are not specialized for any particular prey type (Ellison *et al.* 2009), intra- and interspecific competition still exists (Gibson 1983). Previous work indicated that competitive avoidance resulted in distribution of carnivorous plants by height. However, these findings do not address the potential role of hydrology and soils in niche partitioning among sympatric *Sarracenia*.

With continuously decreasing habitat available for *Sarracenia*, studying the relationships between species distributions and microenvironment is more important than ever for conservation efforts. The objective of this study was to determine the role of hydrogeology and soil classification in driving *Sarracenia* species distributions within the same relatively small geographic area. The hypothesis was that species would be differentially distributed as a result of adaptations to different soil types or water table depths.

Materials & Methods

Study site

Splinter Hill Bog Preserve (SHBP) in Baldwin County, Alabama, which is owned and managed by The Nature Conservancy, was the focus of this research. This location was chosen because it is home to six of the eleven described *Sarracenia* species: *S. flava*, *S. rubra* subsp. *wherryi*, *S. leucophylla*, *S. psittacina*, and *S. rosea*. This diversity made it an ideal location to study sympatry and niche partitioning within native communities (Fig. 1). In 2009, three plots were established on a restored longleaf pine savanna within SHBP (Fig. 2). These savannas are naturally prone to low intensity fires, which aid in nutrient cycling, eradication of non-native species, and promote seed germination for some of the native plants. The sampled savanna was clear-cut in 1996, and at the time our work was completed was annually burned to manage encroachment of woody and invasive species. An old dirt logging road, now used as a hiking trail, splits the savanna site down the center from north to south. Based on observations at the time of sampling, *Sarracenia leucophylla* was evenly distributed throughout this location, while *S. rosea* was found more frequently on the east side of the hiking trail, with fewer individuals near the hiking trail on the west side. *Sarracenia psittacina* was more narrowly distributed on the east side of the trail near the edge of the woods where the soil is more saturated. Putative *S. leucophylla* × *rosea* hybrids were found mainly on the east side of the trail, but were also found infrequently throughout the west side of the trail, where there were no *S. rosea* individuals observed.

SHBP is underlain by the Citronelle Formation (USDA 1964). This formation is of Pliocene age (5.3 to 2.6 Mya; Walker & Geissman 2009), and lies above the Hattiesburg Clay and older forma-

Figure 1: *Sarracenia* species and putative hybrids observed in this study at Splinter Hill Bog, Baldwin County, Alabama, USA. *Sarracenia leucophylla* (top left), *S. rosea* (top right), and putative hybrids (bottom left and right). *Sarracenia psittacina* (not pictured) was present but infrequent in sampled areas.

tions. The Citronelle Formation, consisting primarily of sand, clay, and gravel, is gently sloping towards the Gulf of Mexico. In the SHBP area, elevation typically ranges from 60 to 80 m above sea level. The elevation of SHBP's savanna site ranges from 70 - 60 m above sea level from west to east, with Dyas Creek forming the eastern perimeter. Soil in this area is predominantly sand with

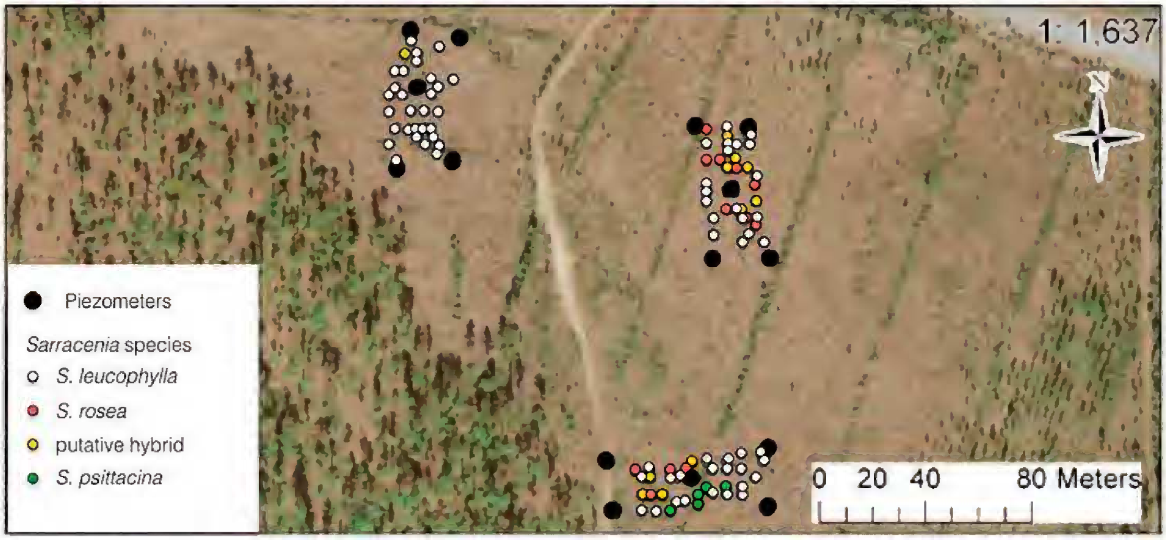

Figure 2: Aerial photo of Splinter Hill Bog Preserve showing plots sampled in the present study. Black circles represent piezometer locations and colored circles represent *Sarracenia* species sampled (white = *S. leucophylla*; red = *S. rosea*; yellow = putative *S. leucophylla* × *rosea* hybrid; and green = *S. psittacina*).

thin layers of clay. All soils are hydric, meaning there is saturation, flooding, or ponding for all or part of a growing season.

Data collection

Three plots were established on a restored longleaf pine savanna at SHBP species identification and mapping (Fig. 2). Approximate distances were measured from the center of one plot to the center of another in ArcMap 10.1 (ESRI). Plots 1 and 2 were approximately 155 m apart, plots 1 and 3 were approximately 125 m apart, and plots 2 and 3 were approximately 215 m apart. Each plot was 50 m × 20 m. Within each plot, four parallel transects were established 5 m apart. Species were recorded every 5 m along each transect, for a total of nine data points per transect and 36 data points per plot (Fig. 2). *Sarracenia* species were identified at each data point along each transect (if no plant was present, the closest *Sarracenia* was sampled), such that a maximum of 36 individual plants were sampled within each plot for a total of 108 individual plants over three plots. Species were identified using the taxonomy of Schnell (1998) and Naczi *et al.* (1999), permanently numbered with aluminum tags, and documented using digital photography.

Soil core samples were obtained from each corner and the center of each study plot (five cores per plot, 15 cores across all three plots). Approximately 30 - 60 cm of core was obtained using a direct push corer. Core samples were analyzed and classified according to the Unified Soil Classification System (ASTM Standard 2006). Piezometers were placed in each of the core holes to map water table elevation (i.e., piezometric head). Depth to water table was measured three times between 2009 and 2010: first in late September 2009, second in early March 2010, and third in July 2010. Average depth to water table was calculated for each piezometer across these three dates and used to develop figures included here. Additional soil classification data, hydric soils, and elevation data were obtained from the Baldwin County Chamber of Commerce. Water table elevation was interpolated in ArcMap 10.1 (ESRI, Redlands, CA) using data obtained in the field and images from the Baldwin County Chamber of Commerce (Fig. 3).

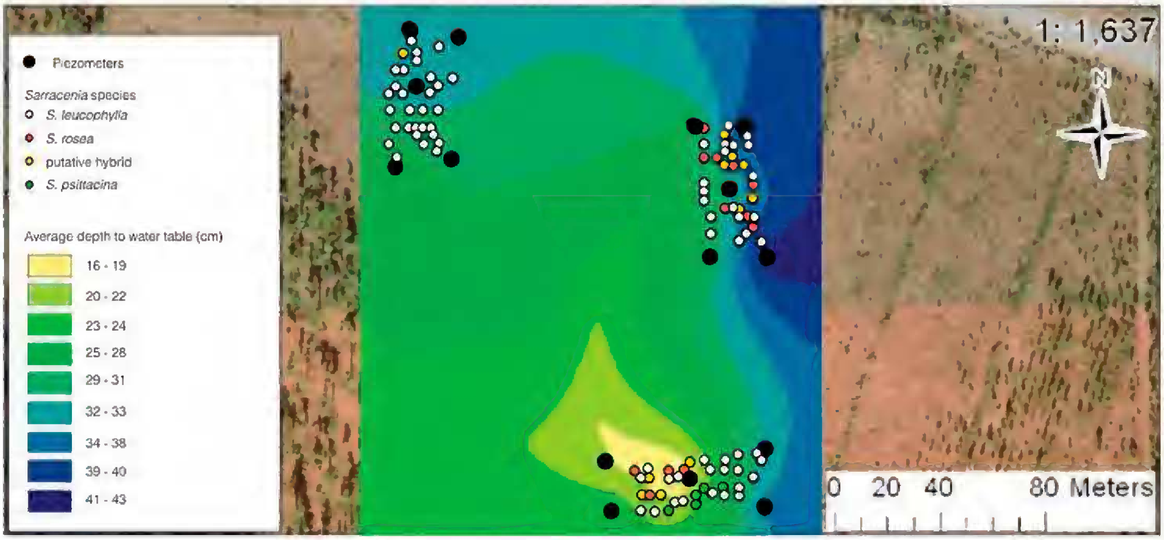

Figure 3: Average water table depths underlying sampling plots at Splinter Hill Bog Preserve. Black circles represent piezometer locations and colored circles represent *Sarracenia* species sampled (white = *S. leucophylla*; red = *S. rosea*; yellow = putative *S. leucophylla* × *rosea* hybrid; and green = *S. psittacina*). Average depth to water table (cm) is illustrated in shades of yellow (shallowest) to dark blue (deepest).

Pearson product-moment correlation coefficient (PPMCC), which measures the linear relationship of two random variables, was employed to evaluate potential correlations between species distribution, water-table elevation, and soil type. This value was determined using Minitab 15 (Minitab, Inc., State College, PA).

Results

Distribution of Sarracenia

Plot 1 contained twenty-one *S. leucophylla*, nine *S. rosea*, and six putative *leucophylla* × *rosea* hybrids. Plot 2 contained thirty-four *S. leucophylla* and two putative *leucophylla* × *rosea* hybrids. Plot 3 contained twenty-two *S. leucophylla*, four *S. rosea*, five *S. psittacina*, and four putative *leucophylla* × *rosea* hybrids. This pattern of species distribution observed within the sampling plots is a good representation of the species distribution in the general area, with the exception of several *S. rosea* individuals on the outskirts of Plot 2 alongside the trail, which did not fall within the parameters of the plot.

Soils

Plot 1 and Plot 3 were in Klej loamy sand with a 0 - 5% slope. This soil type is moderately to well drained, with slow runoff and is strongly acidic in nature (USDA 1964). Plot 2 was partially in Bowie-Lakeland-Cuthbert soils with a 8 - 12% slope, and partially in Plummer loamy sand with a 0 - 5% slope. Bowie-Lakeland-Cuthbert soils are moderately to well drained with fairly rapid runoff, and are acidic to strongly acidic (USDA 1964). Plummer loamy soils are poorly drained, with slow runoff and are strongly acidic (USDA 1964). In Plot 2, only *S. leucophylla* was sampled in the Plummer portion of the plot, while both *S. leucophylla* and putative *S. leucophylla* × *rosea* hybrids were sampled in the Bowie-Lakeland-Cuthbert portion of the plot. A small, but significant correlation between soil type and species distribution was detected by PPMCC analysis across all plots ($r = -0.379$, $p = 0.000$).

Water table elevation

Average depth to water table over the three dates measured in 2009 and 2010 is summarized in Fig. 3. It ranged from 16 cm in the southern portion of the sampling area to 43 cm in the easternmost portion of the sampling area. No significant correlation was detected between water table elevation and species distribution (r = -0.138, p = 0.156). However, correlation between water table elevation and soil type was significant, although low (r = 0.212, p-value = 0.028).

Discussion

Past research has shown that competition for food (in the case of carnivorous plants) and other resources (soil nutrients, water, soil-type preference, *etc.*) are driving factors in the distribuition of closely related *Sarracenia* species of the same height within a population (Gibson 1983). Because of this competition for food, tall pitcher plant species tend to separate from other tall pitcher plant species (e.g., *S. leucophylla* and *S. flava*), but this does not explain the distribution of *Sarracenia* species at SHBP where tall, intermediate, and decumbant species are present in sympatry.

In our study, there was no statistical correlation between water table elevation and species distribution. It is important to note that water table depth varies seasonally and in response to significant rain events in these bogs. Future studies should focus on fluctuations in water table depth throughout the year and how that may relate to niche differentiation in these taxa. The fact that the correlations between soil type and water table elevation, and between soil type and species distribution, were both significant may be evidence of additional relationships between water table depth and species distribution that are yet to be uncovered.

Based on the individuals sampled here, *S. leucophylla* is most abundant and has the widest distribution at SHBP. Putative *S. leucophylla* × *rosea* hybrids seem to be widely distributed across the savanna site at SHBP similar to the putative parent species *S. leucophylla*, rather than the putative parent species *S. rosea*, which has a more restricted distribution. These putative hybrids were observed throughout SHBP, while *S. rosea* were found primarily on the east side of the hiking trail (with a few individuals on the west side closer to the trail). This distribution correlates with water table elevation, which shows *S. rosea* inhabiting areas with a higher water table, whereas the putative hybrids were found throughout. This suggests that hybrid individuals may be better adapted to some microenvironment than one of the parents, which could potentially aid in hybrid speciation. The most localized species sampled was *S. psittacina*, which is known for inhabiting more saturated areas, and is found in the lower elevations of the site where the water table is closest to the surface.

Future research involving more individuals sampled over a greater area, along with the measurement of more environmental parameters (e.g., pH, micro- and macronutrients, microbial activity) would likely yield a more accurate depiction of the influence of environmental parameters on pitcher plant distribution. Given the impacts of urbanization and habitat fragmentation on pitcher plant bogs, it is pertinent to conservation efforts to understand the driving forces of species distribution in remaining habitats, as this information would aid in restoration efforts (Groves 1993).

Acknowledgements: This research was funded by the International Carnivorous Plant Society and the Department of Biology at the University of South Alabama. Brian Barnes was instrumental in early discussions on the development of this research. Tim Sherman, Sinead Ní Chadhain, Smoot Major, and Jim Connors provided insightful comments on previous versions of this manuscript, as well as guidance in the development of the project. Permission to conduct this work was provided by The Nature Conservancy of Alabama.

References

Arnold, M.L., Buckner, C.M., and Robinson, J.J. 1991. Pollen-mediated introgression and hybrid speciation in Louisiana irises. Proceedings of the National Academy of Sciences USA 88: 1398-1402.

ASTM Standard. 2006. Classification of soils for engineering purposes (Unified Soil Classification System) ASTM International, West Conshohocken, PA, 2011, 10.1520/D2487-11.

Carter, R., Boyer, T., McCoy, H., and Londo, A.J. 2006. Community analysis of pitcher plant bogs of the Little River Canyon National Preserve, Alabama. Proceedings of the 13th Biennial Southern Silvicultural Research Conference. Gen. Tech. Rep. SRS-92. Asheville, NC: USDA Forest Service, Southern Research Station. 640 p.

Edwards-Burke, M.A., Hamrick, J.L., and Price, R.A. 1997. Frequency and direction of hybridization in sympatric populations of *Pinus taeda* and *Pinus echinata* (Pinaceae). American Journal of Botany 84: 879-886.

Ellison, A.M., and Gotelli, N.J. 2009. Energetics and the evolution of carnivorous plants – Darwin's "most wonderful plants in the world". Journal of Experimental Botany 60: 19-42.

Ellison, A.M., Butler, E.D., Hicks, E.J., Naczi, R.F.C., Calie, P.J., Bell, C.D., and Davis, C.C. 2012. Phylogeny and biogeography of the carnivorous plant family Sarraceniaceae. PLoS ONE 7(6): e39291. doi:10.1371/journal.pone.0039291.

Furches, M.S., Small, R.L., and Furches, A. 2013. Hybridization leads to interspecific gene flow in *Sarracenia* (Sarraceniaceae). American Journal of Botany 100: 2085-2091.

Gibson, T.C. 1983. Competition, disturbance, and the carnivorous plant community in the southeastern United States. Ph.D. dissertation. University of Utah, Salt Lake City, UT.

Groves, M. 1993. Horticulture, trade and conservation of the genus *Sarracenia* in the southeastern states of America: Proceedings of a Meeting Held at the Atlanta Botanical Garden, September 22-23, 1993. 17 p.

McDaniel, S. 1966. A taxonomic revision of *Sarracenia* (Sarraceniaceae). Ph.D. dissertation. Florida State University, Tallahassee, FL.

Mellichamp, T.L. 2009. Sarraceniaceae Dumortier – Pitcher plant family. Flora of North America: Magnoliophyta – Paeoniaceae to Ericaceae: Volume 8. Oxford University Press. 588 p.

Milne, R.I., Abbott, R.J., Wolff, K., and Chamberlain, D.F. 1999. Hybridization among sympatric species of *Rhododendron* (Ericaceae) in Turkey: morphological and molecular evidence. American Journal of Botany 86: 1776-1785.

Naczi Jr., R.F.C., Soper, E.M., Case Jr., F.W., and Case, R.B. 1999. *Sarracenia rosea* (Sarraceniaceae) a new species of pitcher plant from the southeastern United States. Sida 18: 1183-1206.

Plummer, C.C., McGeary, D., and Carlson, D.H. 2001. Physical Geology 8th edition. McGraw-Hill, New York. 578 p.

Schnell, D.E. 1998. A pitcher key to the genus *Sarracenia* L. (Sarraceniaceae). Castanea 63: 489-492.

Schnell, D.E. 2002. Carnivorous plants of the United States and Canada. Timber Press, Portland. 468 p.

Sheridan, P.M. 2010. Ecological and genetic status of the purple pitcher plant, *Sarracenia purpurea* L., in Maryland and Virginia. Ph.D. dissertation. Old Dominion University, Norfolk, VA.

United States Department of Agriculture. 1964. Soil Survey: Baldwin County Alabama. Series 1960 12: 108.

Walker, J.D., and Geissman, J.W. 2009. Geologic time scale: Geological Society of America. doi: 10.1130/2009.CTS0O4R2C.

Welch, M.E., and Rieseberg, L.H. 2002. Habitat divergence between homoploid hybrid sunflower species, *Helianthus paradoxus* (Asteraceae), and its progenitors. American Journal of Botany 89: 472-478.